

## **The *Euphilotes battoides* complex: recognition of a species and description of a new subspecies. (*Lycaenidae*)**

Rudolf H. T. Mattoni

9620 Heather Road, Beverly Hills, CA 90210, USA

**Abstract.** *Euphilotes bernardino* is recognized as a species separate from *E. battoides*, being cited here as a new combination. A discussion of the background for this action is given, in addition to that for describing a new subspecies, *E. bernardino garthi*, from the Isla de Cedros, Baja California.

### **Introduction**

The paradox of Charles Darwin lay in the title of his immortal work. The crux of Darwin's thesis was that evolution proceeds from the natural selection of individual variants. Epling and Catlin (1950) were among the first to point out that the focus on "origin of species" was largely a result of Darwin's being forced to frame his arguments in taxonomic terminology because of the lack of any knowledge of genetics in his day. They went on to conclude that "Darwin should have emphasized his refutation of the fixity of species," because subsequent workers have unfortunately come to "regard the species not only as a taxonomic category but also as an evolutionary unit." Epling and Catlin conclude that the study of evolutionary processes can only be accomplished by testing individuals because there exist only two vehicles for adaptive change: individuals and breeding populations.

Yet taxonomy does have a vital role in permitting communication, as lucidly pointed out by Murphy and Ehrlich (1984). Biologists simply cannot work without "species," regardless of the merits of the method by which they are defined or other philosophic value they may have, real or imagined. Indeed, the Linnean nomenclatural system works with superb parsimony in providing an index of relationship whether based on phenetic, cladistic, or Gestalt methodology, I believe we all concur on the identity of the vast majority of "species," or clusters of similar appearance, by intuitive recognition of form (Gestalt), at least within the limited geographical areas with which we are familiar. Species identity has come to be "legitimized" by such elegant techniques as chromosome analysis, allozyme quantification, comparative biochemistry, statistical analysis of morphological characters, reproductive compatibility and so forth. A great deal of this work may represent what is a sort of fallacy of misplaced interpretation. Yes, these data do help circumscribe the "species;" and yes, these data are of indisputable

evolutionary significance; and yes, the cladistic concept is a valid approach to infer phylogeny; but no, this doesn't mean the species is a unit of evolution. Ehrlich and colleagues (Ehrlich and Raven, 1959 and Ehrlich and Holm 1962) discussed this subject matter in depth.

A closely related problem of taxonomy has arisen in regard to the utility of a taxonomic nomenclatorial approach to geographic variation within species. Since the landmark work of Wilson and Brown (1953), "subspecies," as the unit of geographic variation, has come to be viewed as arbitrary. The reasoned artificiality of subspecies is lack of concordance among multiple characters when these characters are quantified over the geographic range of variants. Gillam (1956) performed neat analyses of several well known polytypic butterfly species to verify the point. More recently, Hammond (1986) brought the arguments full circle in showing failure of concordance between both "species" and "subspecies" in *Speyeria*, he implies that neither category is more or less arbitrary than the other.

Thus, although taxonomic categories do not explain patterns of variation, categorization is useful for describing patterns of variation. With all organisms, application of names, at all levels, is a matter of responsibility, and will remain inherently controversial. Naming subspecies is no less valid than for any other category when responsibly applied. As a matter of even greater issue today, in the United States, is that subspecies have assumed federal legal status under the Endangered Species Act. The Act provides protection to subspecies of threatened and endangered invertebrates, while uniquely variant populations of vertebrates can be listed. Conversely, a recent decision to not list the butterfly *Speyeria callippe callippe* (Boisduval) was based on the taxonomic assertion by Arnold (1985) that the variant populations proposed for listing did not constitute a valid subspecies. A more recent similar controversy did the result in the listing of *Euphydryas editha bayensis* Sternitzky.

Although arguments continue on both species and subspecies "problems," many represent a sort of continuing reinvention of the wheel. On balance there may be no more or less evolutionary information contained in any taxonomic category. Subspecies particularly serve to highlight patterns of variation which may be of special biological interest.

In the following I will perform some taxonomy, first to formally elevate a subspecies to the species level, because it makes rational sense. Second, I am naming a new subspecies of this species because it represents a large disjunction in appearance and is insular. In the process, the pattern of variation of these butterflies will be reviewed.

### **The species of *Euphilotes***

The genus *Euphilotes* (Mattoni, 1977) was named to circumscribe a group of five species. Later authors familiar with the group variously

recognized three (Shields, 1975, 1977), four (Miller and Brown 1981), or five species (Tilden and Smith 1986). My present interpretation of the genus follows.

The species *E. enoptes* (Bdv.), *battoides*, (Behr), *rita* (B. & McD.), *pallascens* (Tilden & Downey, and *spaldingi* (B. & McD.) constitute five distinct morphospecies each clearly defined by several concordant characters of both male and genitalia and early stage morphology. The latter three species are allopatric, although *spaldingi* overlaps the other two in broad distribution. The three are clearly sister species, but should be regarded as distinct by virtue of several unique characters states. *E. mojave* should be rationally regarded as a species differentiated from *E. enoptes* by small but consistent differences in wing facies, female genitalia, and hostplant preference, in addition to sympatry (with and without synchrony) of several populations with other *enoptes* subspecies. Certain patterns of variation, distribution and natural history in the *E. battoides* set of entities imply a single species concept here cannot palpably describe the observed pattern of variation.

*E. battoides* is distinguished from its congeners at least by male and female genitalia, egg chorion morphology (Mattoni, unpubl.), fourth instar larva chaetotaxy and pattern (Ballmer and Pratt, 1988) and obligate univoltinism. As with all species of *Euphilotes*, populations are delimited by the spacial distribution and flowering times of their usually specific *Eriogonum* hostplants (see Shields, 1975). A number of subspecies have been described to reflect this variation. These are summarized as follows, with hostplant data from Shields (1975, 1977) and Pratt (unpubl.)

subspecies	distribution	flight time	<i>Eriogonum</i> hostplant
<i>battoides</i> (Behr)	Alpine Sierra, CA	July, Aug.	<i>lobbii</i> , <i>incanum</i> , <i>polypodium</i>
<i>oregonensis</i> (B. & McD.)	Casoades, OR	July	<i>marifolium</i> , <i>umbellatum</i>
<i>intermedia</i> (B. & McD.)	No. CA, So, OR	July	<i>marifolium</i> , <i>incanum</i>
<i>glaucon</i> (W.H. Edws)	E. CA, WA, OR, ID, MT, NV, B.C.	May-July	<i>umbellatum</i> , <i>heracloides flavum</i> , <i>sphaerocephalum</i>
<i>comstocki</i> (Shields)	Tehachapi Mts. CA	Aug	<i>umbellatum</i>
<i>centralis</i> (B. & McD.)	CO, UT, NM, AZ	July-Aug	<i>umbellatum</i> , <i>jamesi corymbosum</i>
<i>baueri</i> (Shields)	CA, NV	May	<i>ovaliflorium</i> , <i>kennedyi</i>
<i>bernardinio</i> (B & McD)	S & Cent CA, Baja CA	Apr-July	<i>fasciculatum</i> , <i>cinereum</i>
<i>martini</i> (Mattoni)	Mojave; CA, AZ	Apr-May	<i>fasciculatum</i>
<i>allyni</i> (Shields)	EI Seg. Dunes, CA	July-Aug	<i>parvifolium</i>
<i>garthi</i> (new)	Cedros Island, Baja CA	Mar-June	<i>fasciculatum</i>
<i>ellisi</i> (Shields)	E. CA, NV, AZ, CO, UT	July-Sept	<i>corymbosum</i> , <i>heermannii</i> , <i>microthecum heermannii</i>

The relationships among the above taxa are more complex than given and may be more accurately dealt with as several species. The model of one monophyletic grouping exhibiting simple geographic polytypy does not square with the data: e.g. sympatry and synchrony of *battoides* and *intermedia* at Gold Lake, CA, sympatry and allochrony of *glaucon* and *baueri* at Westgard Pass, CA; sympatry and allochrony of *martini* and



*ellisi* in several mojave desert range; sympatry and allochrony of *ellisi* and an undescribed taxon in northern Arizona, and the parapatry (sympatry?) and synchrony of *glaucon* and *bernardino* at several sites along the east slope of the southern Sierra Nevada. As an initial step in attempting to more clearly reflect the pattern of variation in the group, I propose the following concept:

*Euphilotes bernardino* (Barnes & McDonnough 1917) new combination

The species includes the cluster of four closely related taxa commonly recognized as subspecies of *battoides*: *bernardino* (B. & B. 1917), *martini* (Mattoni, 1954), *allyni* (Shields, 1975), and *garthi* (new spp.). Synapomorphic characters of the species include: 1) exclusive hostplants *Eriogonum fasciculatum*, *E. cinerium*, and *E. parvofolium* 2) small mean adult size (wingspan <11.0 mm) and 3) fourth instar larva morphology and pattern (Pratt, unpub.). The suite of variable wing pattern characters which discriminate the four subspecies is given in Table 1.

Although recognition of *E. bernardino* as a "species" is based on weak wing characters, size and larval hostplant, and larval characters which may not stand up to scrutiny of the many populations not surveyed, the sympatric criterion is consistent. Future work may well discriminate other species in the remaining "*battoides*" group. The taxon *glaucon*, for example, passes the sympatry test in some localities has a large geographic distribution, shows extensive wing pattern variation, and uses several foodplants. Complete information on *glaucon* over its range and in relation to its nearest neighbors is not sufficient to override the consideration of conservatism.

### Classification of the populations of *E. bernardino* INTRAPOPULATION VARIATION AND WING PATTERN TERMINOLOGY

The degree of variation in wing pattern elements in adult *Euphilotes* is shown in Figure 1. Pairs of specimens were selected from five series of both *E. enoptes* and *E. battoides* to show extremes of both upper and underside variation in both sexes. Such extremes are frequent when dealing with series and underline the care that should be taken in arriving at taxonomic decision in the group of butterflies.

The description of wing characters in polyommata blues has been very inconsistent in the past for lack of a standardized nomenclature to apply to the various elements of pattern which repeat through the group. Nabokov (1943) attempted to rectify the matter by suggesting a detailed terminology. I have in large part followed his system, which is graphically presented as figure 2. Interspaces are designated by the named vein anterior to the space. The lower part of figure 2 diagrammatically classifies fringe types which are found throughout the tribe



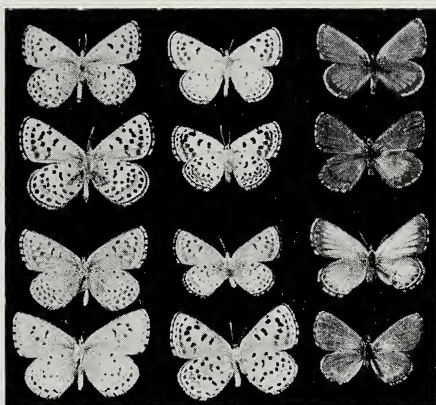


Fig. 1. Intrapopulation variation exhibited by selected pairs of *Euphilotes*.  
**Top two rows**, left to right. *E. enoptes ancilla*, ♀ UNS. Montana, 9 mile canyon, 20 vi 82. S. Kohler. *E. pallescens pallescens*. ♀ UNS. Nevada, Lincoln Co. 2 mi NE Hancock Summit, 24 viii 78, O. Shields. *E. battoides centralis*, ♂ UPS. Colorado, Chaffee Co. O'Haver Lake, 30 vi 68, R. Mattoni.  
**Bottom two rows**. *E. Battoides intermedia*, ♂ UNS, California, Siskiyou Co. Castle Lake, 21 vii 77, T. Dimock. *E. battoides ellisi*, ♀ UNS. Arizona, Coconino Co. 9 mi. E. Winona, 20 viii 79, R. & L. Mattoni. *E. battoides baueri*, ♀ UPS. California, Inyo Co. White Mt. Rd. 2. mi. N. Hwy. 168. 5 vi 76, R. & N. Mattoni.

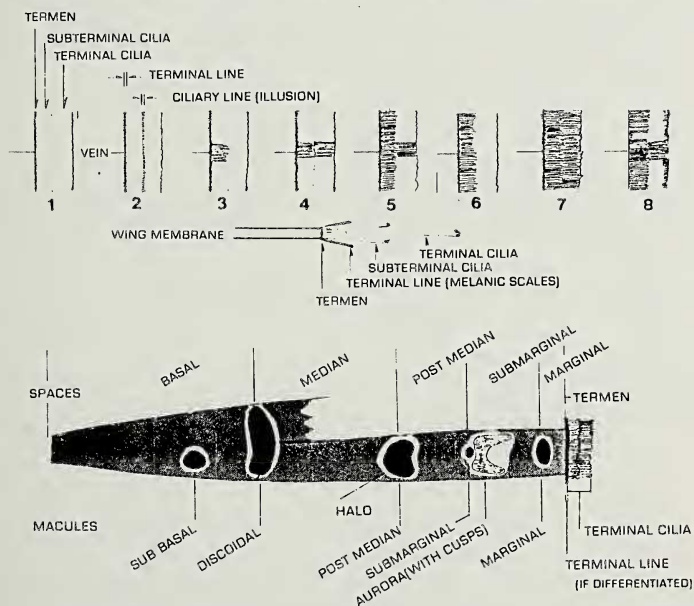


Fig. 2. **Upper**. Nomenclature for wing pattern elements in *Euphilotes* (and most Polyommata blues). Diagrammatic representation of UNH macules and marks across  $M_1$  (cut-away) and  $M_2$ . Interspaces named for anterior vein.  
**Lower**. Fringe types as character states at  $CU_1$ .

Table 1. Comparative data of samples of populations of *Euphilotes battoides*: *garthi* (type series, data in text), *allyni* (ES = CA, Los Angeles Co., El Segundo Dunes, Chevron Refinery, 25 VII 65, Mattoni, leg.), *allyni* (PV = CA, Los Angeles Co., Palos Verdes Peninsula, Crenshaw, 27 VII 83, Mattoni, leg.), *bernardino* (CA, Los Angeles Co., Santa Monica Mts., Mulholland Dr. & Sepulveda, various dates, Mattoni, leg.), *martini* (AZ, Yavapai Co. I-17 at Bumblebeecutoff, 17 IV 79, Mattoni, leg.). *f.* = Frequency. Boldface numbers indicate character state sets unique to that subspecies. Refer to Fig. 2 for numeration.

		<i>garthi</i>	<i>allyni</i> ES	<i>allyni</i> PV	<i>bernardino</i>	<i>martini</i>
<b>Wingspread-mm</b>						
Males	Mean	10.1	10.3	10.8	10.0	10.9
	Range	8.7-10.9	9.4-11.0	10.0-11.5	9.3-10.5	10.0-12.3
	N	11	10	10	7	11
Females	Mean	9.9	10.0	10.3	9.5	10.7
	Range	9.4-10.4	9.4-10.5	9.8-10.9	8.5-10.2	9.9-12.0
	N	5	10	10	8	10
<b>Males-Upperside</b>						
FW-Marginal		1.26	1.10	1.01	0.59	0.86
Bandwidth-mm						
HW-f. with aurora		1.0	0.8	0.9	0.1	0.3
f. with checkered fringe M <sub>3</sub>		1.0	0	0	0	0.7
<b>Underside</b>						
f. with halos		0	0	0	0	0.8
FW-width PM macule mm M		1.20	0.99	1.00	0.80	0.70
f. dissociated PM macs.		0	0.6	0.9	0.7	1.0
f. without marg. mac. R <sub>4+5</sub>		0.5	0.9	0.4	0.3	0.5
f. Cu <sub>2</sub> Suffusion		0.5	0	0.1	0	0.6
HW-f. dissociated aurora		1.0	10	1.0	0.7	0.2
f. fringe type 4		0.7	0	0.1	0	0
<b>Females-Upperside</b>						
HW-width aurora M <sub>3</sub> mm		0.88	1.59	1.87	1.50	0.96
f. distinct marg. macs.		0.2	1.0	1.0	1.0	0.8
<b>Underside</b>						
f. with halos		0	0	0	0	0.5
FW-width PM mac. mm M		1.43	1.09	1.13	0.93	0.85
f. with aurora		0.2	0.9	0.8	0.5	0.6
f. dissociated PM macs.		0	0.2	0.3	0.4	1.0
f. without marg. mac. R <sub>4+5</sub>		1.0	0.6	0.1	0.5	0.4
f. Cu <sub>2</sub> Suffusion		0.6	0.7	0.7	0	0.4
HW-f. dissociated aurora		1.0	1.0	1.0	0.7	0.2
f. fringe type 4		0.8	0.1	0.1	0	0
Foodplant		fasciculatum	parvifolium	cinereum	fasciculatum	fasciculatum

## Notes

- allyni* ♂ homoecotic DV transposition of cyanic scales over distal part of Cu<sub>2</sub>-UNF.
- martini* dimorphic for an elongated tear shaped postero-distal pointed UNF PM macule in M<sub>2</sub> in .3 males and .8 females and subsequently noted in other population of *martini*.

and are useful characters. The cross section of the termen illustrates how the illusion of various fringe patterns is produced. The set of character states used in this study are given in Table 1.

Fig. 3. Subspecies of *Euphilotes bernardino*. UPS, 4 specimens above, UNS the same 4 specimens below. About 0.9 life size.

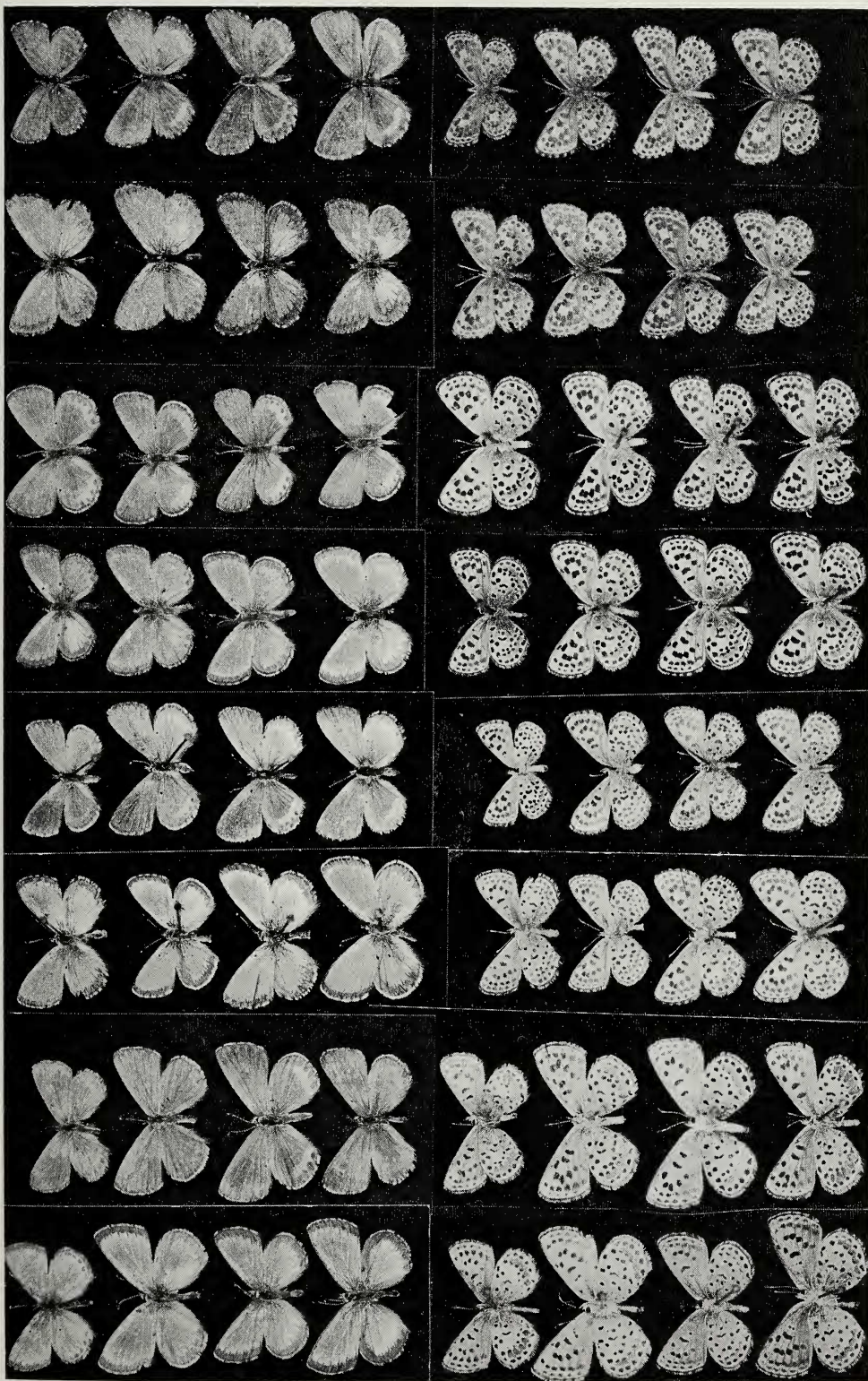
Rows 1 and 2, ♂ and ♀ *E. b. martini*, Arizona, Yavapai Co. Bumblebee turnoff of 1-17, 17 iv 79 R. Mattoni.

Rows 3 and 4, ♂ and ♀ *E. b. bernardino*. California, Los Angeles Co. Mulholland Hwy. various dates, May, R. Mattoni.

Rows 5 and 6, ♂ and ♀ *E. b. allyni*, California, Los Angeles Co. Chevron plant, El Segundo, 25 vii 65. R. Mattoni.

Rows 7 and 8, ♂ and ♀ *E. b. garthi* from type series: see data in text.







### Relationship of subspecies

There are 4 subspecies of *E. bernardino* (Table 1). Of these, one has not been formally described, although recognized for some time (Rindge, 1948):

#### *Euphilotes bernardino garthi* Mattoni *new subspecies*

**Males.** Fig. 3. Table 1. Distinguishable in every specimen available from all other subspecies by 1) UPF marginal bandwidth, 2) UPH marginal band not dissociated, 3) UNS macules, particularly the post median (PM) set, extremely large, PM set arranged without dissociation between interspaces, 4) UNH fringe type 4.

**Females.** Fig. 3. Table 1. Distinguishable in all specimens by 1) UPH aurora not extending distally to wing margin such that marginal macules are not differentiated, 2) underside characters as in males.

**Genitalia.** Indistinguishable in either sex from any member of the *E. battoides* complex.

**Type material.** Holotype male, Baja California Norte, Isla de Cedros, canyons west of Punta Norte, 1 IV 1983 (Faulkner and Brown). Paratypes some locality as holotype, dates as follows: 2 ♂♂ 30/III, 4 ♂♂ 4 ♀♀ 1/IV, 1 ♂ 2/IV, 1 ♂ 1 ♀ 1/VII, 2 ♂♂ 3/VII, all 1983 all leg. Faulkner and Brown. 3 ♂♂ "Mexico, Cedros Island, 15/III/39" no. leg cited (presumably F. Rindge) colln. LACMNH. **Disposition of types.** Holotype, 5 male paratypes and 4 female paratypes deposited in the SDNHM; 1 male and 1 female paratype deposited in CAS, San Francisco; 3 male and 1 female paratypes deposited in the LACMNH; 1 male and 1 female paratype deposited in the Instituto de Biología, National University of Mexico, Mexico City; 1 male and 1 female deposited in the USNM, Washington.

**Distribution.** *E. bernardino garthi* is an apparent disjunct population of the species endemic to Cedros Island. Although the indicated larval hostplant occurs throughout the island, the insect was only found in March and April at low elevations in the washes and canyons of the north end of the island, and at higher elevations in July.

**Natural History.** The larval hostplant in all likelihood is *Eriogonum fasciculatum* Bentham with which the adults were exclusively associated. The insect also appears univoltine, with an extended emergence taking place as the season extends altitudinally. This pattern corresponds to the development of foodplant flowering which is essential for adult nectaring, oviposition, and larval growth. A report of Faulkner and Brown discusses Cedros Island and its butterfly fauna in detail.

**Etymology.** The subspecies nomen is a patronym honoring Dr. John Garth for his early work on the biology of Baja California and especially Isla de Cedros.

## Discussion

*E. bernardino garthi* is an endemic of Isla de Cedros, where it probably evolved in isolation since the eustatic sea level rise after the last glaciation. Indications of evolutionary history might be inferred from study of any *E. bernardino* populations their foodplants on the adjacent mainland, Natividad island which was also connected to the mainland, and San Benito island which is oceanic. Simultaneously, insight might be shed on the emigration potential of *Euphilotes*, which is unknown from all the Channel Islands (Miller, 1985), although Santa Rosa and Catalina islands have populations of proper foodplants.

Quantitative data on wing characters, determined to be variable over the whole array of *Euphilotes* species, are given for the four subspecies of *E. bernardino* in Table 1. Certain character states can be used to classify all specimens of the species almost unequivocally into an appropriate subspecies following Table 1. The single character state which may serve to identify each taxon is the relative amount of melanin in the underside macules. The character is expressed by the width of the PM macule of forewing  $M_3$  in in table 1. I illustrate the character in a short series of specimens of each taxon in figure 3, which also provides information on variability in wing pattern as well as other characters. The cline of increasing darkening exhibited by each subspecies from the desert to coastal environments is concordant with two additional characters of the males: 1) upperside cyanic overlay and 2) marginal band width. It must be emphasized that these clines are sharp step clines, with the steps corresponding to the subspecies limits. *E. bernardino bernardino* populations on the desert edges of the San Bernardino and San Jacinto mountains appear somewhat lighter than cis-montane populations, but these are not clinal in other traits which might confuse them with *martini*. Scoring individuals from *bernardino* colonies at Lytle Creek (south side of the San Gabriel mountains) and Horsethief Canyon (north side of the San Bernardino range) showed them to be statistically identical in character states to the data given in Table 1.

The two darkest subspecies, *garthi* and *allyni*, are associated with hot daytime weather during their flight times, with most moisture coming from frequent dense fogs and not rainfall. The two no doubt evolved independently under what may be similar environmental conditions, the intervening 700 km are occupied by populations of *bernardino*.

The distribution of the four subspecies is shown in figure 4. The data are largely from Shields (1977) plus a few newer records. The occurrence of *bernardino* is probably almost continuous, corresponding with the continuous distribution of its hostplant *Eriogonum fesciculatum* across most of southern California. However, following the coast ranges north of Santa Barbara the hostplant becomes increasingly disjunct. The

subspecies *martini* is completely disjunct, nowhere directly meeting *bernardino*. Through the desert mountains of eastern California, southern Nevada, and western Arizona, *martini* occurs as a series of isolated colonies. From central Arizona east it is more continuous as it occurs over the belt of *Eriogonum fasciculatum* which grows in a band along the south slope of the Mogollon Plateau and then ranging into southern Arizona and probably Sonora.

The precise distributional boundaries of *bernardino* are not defined where it ranges into west central Nevada. The two populations in fig. 4 were cited by Shields (1977) from Churchill Co., who made the specimens available. Although highly suggestive of *bernardino*, they must remain unassigned until further collections are available. The populations were associated with *Eriogonum heermanii* and Austin (pers comm.) found similar populations, also on *E. heermanii*, in the southern Toiyabe mountains. These represent the first documentation of *Euphilotes bernardino* on *Eriogonum heermanii*.

Across the area which would provide any contact zone between *Euphilotes bernardino bernardino* and *E. b. martini*, populations are found as isolates in desert mountain "islands." There are no data, other than anecdotal, to indicate the two "blend" in any manner as suggested by both Langston (1969) and Shields (1977). The Beatty, Nye County (Shields, 1977) specimens were scored and completely overlap the data given in Table 1, including dimorphism for the same peculiar PM macule as cited. The *martini* population of the Providence Mountains was also identical by the same criteria. The term "blend" is a very unfortunate term which has found its way into wide use in the literature. By implication "blend" is usually taken to mean the result of gene flow causing blending of character states. However, in all but the most rigorously tested cases, it is not possible to discriminate between hybridization or introgression and adaptive selection along an environmental gradient (Endler, 1977), but see Collins (1984) for a well documented study in the Lepidoptera.

The fine grain distribution of the *bernardino* and *allyni* interface is well established, although precise classification of the interface population (s) is open to interpretation. *E. bernardino allyni* occurs only on the historic El Segundo sand dunes, which comprised four distinct segments prior to the urbanized destruction of southern California. It is extinct on two segments (Mattoni, 1989). It is solely restricted to *Eriogonum parvifolium* as larval hostplant, although females will oviposit on both *E. cinereum* and *fasciculatum* in field and choice experiments. Mattoni (unpub.) has evidence that the latter two species are toxic to neonate larvae from El Segundo Dunes stock. Today *Euphilotes bernardino allyni* is known from only three sites: 1) the 1 Ha type locality at the Chevron refinery preserve, 2) on about 10 Ha at the Los Angeles International Airport (LAX) dunes property and 3) on a <0.5 Ha site at Malaga cove. The latter, at the northwest base of the Palos Verdes



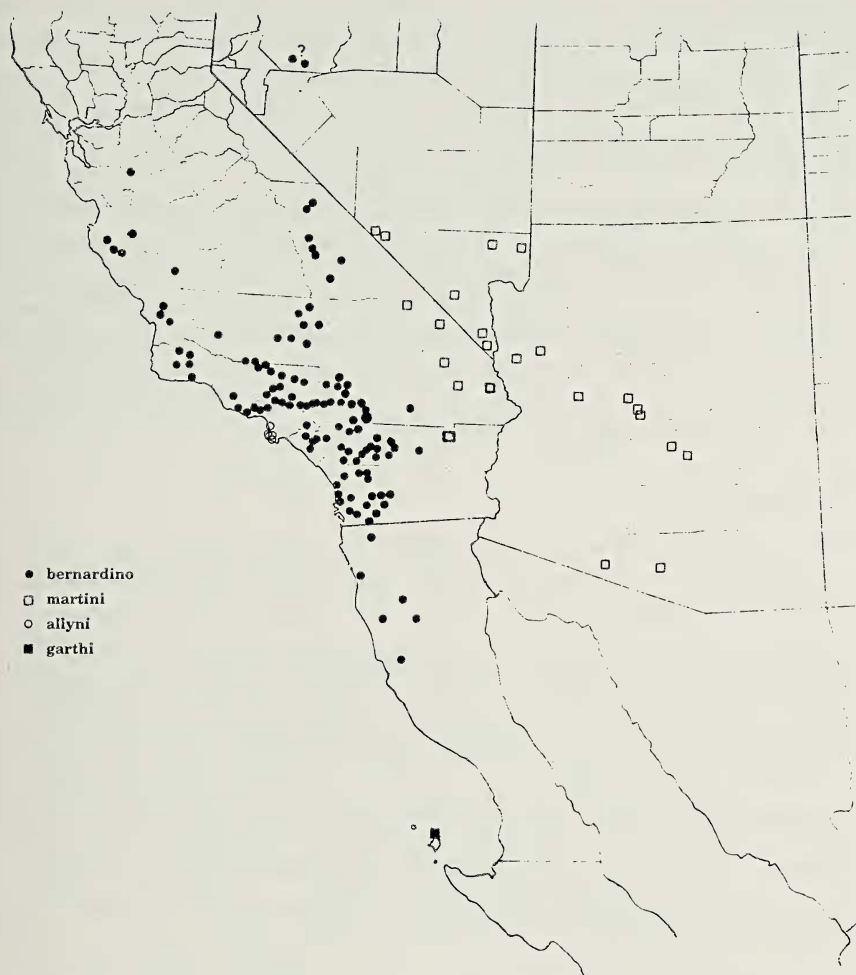


Fig. 4. Distribution map of *E. bernardino* and its subspecies discussed in text

peninsula, is isolated by one kilometer from the south where the buckwheat *Eriogonum cinereum* becomes common, growing intermixed with *E. parvifolium* along the seacliff. At this point there is a shift in butterfly ecotype to a taxon which is best referred to *bernardino* on the basis of natural history, although phenetically it overlaps the wing pattern of *allyni*. At the higher elevations on Palos Verdes, the host-plant occurs as pure stands of *E. cinereum*, but also includes a few colonies of *E. fasciculatum* which grown in the canyons of the north slope. It is not known if the butterfly feeds on the latter plant.

Examination of the topographic survey maps, and aerial and other photographs taken prior to significant urbanization in the 1930's showed that the scrub communities of both the El Segundo Dunes and

the Palos Verdes peninsula were surrounded and isolated by low forb meadows. Further, the peninsula was isolated from the major dunes site. The latter is reflected in two butterfly distributions: the now extinct Palos Verdes Blue, *Glaucopsyche lygdamus palosverdesensis* Perkins and Emmel, which evolved independently from *G.l. australis* Grinnell, a still abundant species on the dunes; and the occurrence of an *Apodemia mormo virgulti* (Behr) ecotype on the dunes which is absent from Palos Verdes. These findings indicate that the *Euphilotes bernardino bernardino* populations found today at Palos Verdes are relicts from some time since the last glaciation when a continuous belt of *Eriogonum fasciculatum* must have connected to the coastal sage communities to the north. *Euphilotes bernardino allyni* on the other hand must have evolved in situ and in isolation during the formation of the El Segundo sand dunes over the past 4–6000 years.

### Conclusions

The nature, meaning and proper use of species and subspecies concepts will no doubt remain an idle and infinite speculative endeavor. However, for the purposes of the above description of patterns of variation of the *bernardino* part of the *E. battoides* complex, the general application of kind (species) and reasonably concordant geographically distributed kind (subspecies) suffices. There is no evolutionary connotation inherent in either category itself, although two modal sorts of subspecies variant classes are included: *bernardino* and *martini* with large geographic distributions and inclusion of many probable ecotypic clusters (genetically differentiated populations adapted to local environmental conditions), and *allyni* and *garthi* which are highly restricted endemic populations each of which may be, or recently were, essentially panmictic.

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### Literature Cited

- ARONLD, R. A., 1985. Geographic Variation in Natural Populations of *Speyeria callippe* (Boisduval) (Lepidoptera: Nymphalidae). Pan Pac. Entom. 61:1-23.
- BALLMER, G. & G. PRATT, 1989. A Survey of the Last Instar Larvae of the Lycaenidae of California. J. Res. Lepid. 27:1-82.
- COLLINS, M. M., Genetics and Ecology fo a Hybrid Zone in Hyalophora (Lepidoptera: Saturniidae). Univ. Calif. Publ. Entom. vol. 104: 93p. Berkeley.

- EHRlich, P. R. & R. W. HOLM, 1962. Patterns and Populations. *Science* 158: 652-657
- EHRlich, P. R. & P. RAVEN, 1969. The Differentiation of Populations. *Science* 165:1228-1232.
- ENDLER, J. A., 1977. Geographic Variation, Speciation, and Clines. Princeton Univ. Press. NJ.
- EPLING, C. & W. CATLIN, 1950. The Relation of Taxonomic Method to the Explanation of Organic Evolution. *Heredity* 4:313-325.
- FAULKNER, D. & J. BROWN, 1989. Butterflies of Isla de Cedros, Baja California Norte, Mexico. *J. Res. Lepid.* 27:
- GILLHAM, N. W., 1956. Geographic Variation and the Subspecies Concept in Butterflies. *Syst. Zool.* 5:110-120.
- HAMMOND, P. C., 1986. A Rebuttal to the Arnold Classification of *Speyeria callippe* (Nymphalidae) and the defense of the subspecies concept. *J. Res., Lepid.* 24:197-208.
- LANGSTON, R. L., 1969. *Philotes* of North America: America: A Synonymic List and Distribution (Lycaenidae). *J. Lepid. Soc.* 23:49-62.
- MATTONI, R. H. T., 1989. The endangered El Segundo Blue Butterfly. Unpublished.
- MILLER, S., 1985 (1968). Butterflies of the California Channel Islands. *J. Res. Lepid.* 23:282-296.
- MURPHY, D. D. & P. R. EHRlich, 1984. On Butterfly Taxonomy. *J. Res. Lepid.* 23:19-23
- NABOKOV, V., 1944. Notes on the Morphology of the Genus *Lycaeides* (Lycaenidae: Lepidoptera). *Psyche* 51:104-138
- RINDGE, F., 1948. Contributions Toward a Knowledge of the Insect Fauna of Lower California. No. 8. Lepidoptera: Rhopalocera. *Proc. Cal. Acad. Sci.* 4th series 24:298-312.
- SHIELDS, O., 1975. Studies on North American *Philotes* IV. Taxonomic and Biological Notes, and New Subspecies. *Bull. Allyn Museum* No. 28. 36 pp.
- , 1977. Studies on North American *Philotes* (Lycaenidae) V. Taxonomic and Biological Notes, continued. *J. Res. Lepid.* 16-1-67.
- TILDEN, J. W. & A. C. SMITH, 1986. A Field Guide to the Western Butterflies. Houghton Mifflin, Boston.
- WILSON, E. O. & W. L. BROWN, 1953. The subspecies concept and its taxonomic application. *Syst. Zool.* 2:97-111.

Note added in proof: A recent paper by O. Shields and J. Reveal (1988. Sequential evolution of *Euphilotes* (Lycaenidae, Scolitantidini) on their plant host *Eriogonum* (Polygonaceae; Eriogonoideae). *J. Linn. Soc.* 33:51-91) was received after this paper was in final proof. Shields proposed therein to elevate *bernardino* to species status, an action supported by the above, with the exception of *E. battoides ellisi*. This combination is illogical because of sympatry (but allochrony) with *E. bernardino martini*. Consideration of *ellisi* as a subspecies of *bernardino* is insupportable because of chaetotaxy (Pratt, unpublished), foodplant, adult pattern and size, and seasonal adaptedness. These characters firmly place it in the *battoides* group.